NEKTON IN GULF COAST WETLANDS: FINE-SCALE DISTRIBUTIONS, LANDSCAPE PATTERNS, AND RESTORATION IMPLICATIONS

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Abstract. Many decapod crustaceans and fishes are common inhabitants of flooded salt marshes in the northwestern Gulf of Mexico, but spatial distributions are uneven, and population sizes are difficult to estimate. We measured fine-scale (1–10 m) distributions of nekton on the vegetated marsh surface using enclosure samplers in Galveston Bay, Texas, and used these patterns to estimate population size. Natant decapod crustaceans were abundant in the marsh; densities of juvenile brown shrimp *Farfantepenaeus aztecus*, white shrimp *Litopenaeus setiferus*, and blue crabs *Callinectes sapidus* were highest 1 m from the water's edge and declined rapidly to 10 m from the edge. We developed regression models to describe these fine-scale density patterns and validated the models with independent data on density distributions from two other marsh systems. We used a Geographic Information System to transfer the density models to a natural marsh landscape; the highly fragmented Elmgrove Point marsh was composed of shallow nonvegetated bottom (37.4% of the area) and *Spartina alterniflora* vegetation (62.6%) with ~15% of the vegetated area within 1 m of the marsh–water interface. We estimated that this 437-ha salt marsh complex supported populations of 16.2 million brown shrimp, 15.5 million white shrimp, and 11.3 million blue crabs. We divided the marsh complex into 39 sectors and examined relationships between nekton populations and landscape-scale patterns of marsh fragmentation. The amount of edge and the population estimates in a sector increased consistently with the amount of water up to ~20–25%. Nekton population declines were not apparent until the late stages of marsh disintegration (>70% open water). We also used our fine-scale density models to simulate the effects of adding creeks to a 1-ha created salt marsh of solid vegetation. For shrimp, 1–2 creeks/ha (or a comparable amount of edge) were required to reach populations equivalent to shallow nonvegetated bottom, and up to 6 creeks/ha were required to reach populations similar to those estimated for the natural marsh complex. Simulated populations of blue crabs reached levels in the natural marsh complex with the addition of fewer creeks (2–3 creeks/ha).

Key words: blue crabs; density models; edge marsh; Gulf Coast wetlands; habitat fragmentation; landscape patterns; nekton populations; restoration; salt marsh; shrimp; Spartina alterniflora; *tidal creeks.*

INTRODUCTION

Juvenile penaeid shrimps, blue crabs, and other nekton are abundant in coastal salt marshes of the northwestern Gulf of Mexico (Zimmerman and Minello 1984, Minello 1999, Zimmerman et al. 2000); but complex distribution patterns at various spatial scales make it difficult to estimate population sizes. Densities are seldom distributed evenly over the vegetated marsh surface, and some species aggregate near the marsh vegetation–water interface or the marsh edge (Baltz et al. 1993, Minello et al. 1994, Peterson and Turner 1994, Rozas and Zimmerman 2000). To estimate population sizes, these fine-scale (1–10 m) density patterns must be interpreted in the context of landscape-scale patterns of marsh vegetation interspersed with tidal creeks and ponds.

Many nekton species in this region appear dependent on wetlands as nurseries (Boesch and Turner 1984, Deegan et al. 2000, Zimmerman et al. 2000), and these nurs-

eries are threatened by extensive wetland loss (Gagliano et al. 1981, Bauman et al. 1984). Thus, some species are literally and figuratively living on the edge. Wetland loss is caused by a variety of factors, but coastal submergence and increasing inundation patterns appear to be important (Sasser et al. 1986, Britsch and Dunbar 1993, Turner 1997, Day et al. 2000). Up to a point, factors that cause wetland loss may also increase the value of wetlands and their use by natant species (Zimmerman et al. 2000). Relationships between nekton populations and patterns of marsh degradation and fragmentation may be useful in understanding the linkages between wetlands and nekton and the implications of landscape-scale loss of this habitat (Browder et al. 1989).

The extent of wetland loss in the northern Gulf also has intensified efforts to create new wetlands, and there is a need to develop design criteria to optimize the value of these wetlands for nekton. Many created wetlands appear topographically simple, with little variability in elevation and with few creeks and ponds (Delaney et al. 2000, Shafer and Streever 2000). This lack of interspersion between marsh and water has serious im-

plications for nekton use. The addition of edge to created wetlands can likely improve their value for nekton (Minello et al. 1994), but the optimal amount and configuration of this added edge has not been determined.

Previous studies on Gulf Coast marshes have identified a general pattern of high nekton densities near the marsh edge (Baltz et al. 1993, Minello et al. 1994, Peterson and Turner 1994, Minello 1999, Rozas and Zimmerman 2000). Our objectives in this study were to examine these nekton distributions in more detail and apply this information to population estimates. We focused our efforts on juvenile brown shrimp *Farfantepenaeus aztecus* (formerly *Penaeus aztecus*, see Perez Farfante and Kensley 1997), white shrimp *Litopenaeus setiferus* (formerly *Penaeus setiferus*, see Perez Farfante and Kensley 1997), and blue crabs *Callinectes sapidus*, because these species are commercially important, relatively abundant, and consistently concentrated along the marsh edge. We developed regression models to describe fine-scale (1–10 m) density patterns on the marsh surface and used a Geographic Information System to transfer the density models to a natural marsh landscape and estimate nekton population sizes. We also looked at relationships between nekton populations and landscape-scale patterns of marsh and water; these marsh–water patterns may be related to fragmentation of the marsh complex (Browder et al. 1985). In addition, we used our fine-scale density models to simulate nekton population changes associated with adding edge to a created salt marsh. Throughout, we define the marsh surface as the vegetated area of a marsh complex; the marsh complex or system includes the vegetation along with spatially interspersed shallow nonvegetated bottom (SNVB) including tidal creeks and ponds. Marsh edge is the interface between the vegetated marsh surface and SNVB in the marsh complex.

METHODS

Gang's Bayou sampling

We sampled nekton on the marsh surface during the spring (30 May–1 June) and fall (3–4 October) of 1995 in a marsh dominated by *Spartina alterniflora*. The marsh was located near Gang's Bayou in the Galveston Bay system, Texas (Fig. 1), and the area sampled included 1 km of shoreline surrounding a small marsh pond. The pond was connected to Gang's Bayou and West Bay by several small bayous that remained flooded even on low tide. We selected this area because the slope of the vegetated shoreline varied, the vegetated marsh surface extended at least 20-m from the edge of the pond, and this fringing marsh surface had substantial areas of solid vegetation without extensive small ponds and creeks. The marsh edge was identified as the interface between the marsh vegetation and the open water of this pond.

We used an enclosure device (drop sampler) to sample nekton following methods developed by Zimmerman et al. (1984). The sampler is a fiberglass and steel cylinder (1.14 m diameter) that is dropped from a boom on a shallow-draft boat enclosing organisms in a 1-m² area. Unlike much gear, this sampler is effective in dense emergent vegetation and can provide estimates of nekton density at specific locations within a marsh (Rozas and Minello 1997). During both the spring and fall, we collected 10 randomly located enclosure samples on the marsh surface at each of four distances from the edge (1, 3, 5, and 10 m into the vegetation). These seasons were chosen because large numbers of young penaeid shrimps, blue crabs, and fishes recruit into the Galveston Bay system at these times and are present on the marsh surface.

Sampling was conducted during the day at high tide when the marsh vegetation was flooded. After the sampler was in place, we measured water depth, temperature, dissolved oxygen, and salinity within the enclosure (see Rozas and Zimmerman 2000 for details). Water samples were collected for turbidity and analyzed in the laboratory using a nephelometer (Model DRT-100B turbidimeter, H.F. Scientific, Incorporated, Fort Myers, Florida) calibrated with a formazin standard (formazin turbidity units; FTU). *Spartina* stems were clipped, and most of the natant macrofauna trapped in the sampler was removed using dip nets while the water was pumped out of the enclosure and through a 1-mm mesh net. When the sampler was completely drained, animals remaining on the bottom were picked up by hand. The collection was preserved in formalin with Rose Bengal stain. In the laboratory, the samples were sorted; and fishes, crustaceans, and molluscs were identified to the lowest feasible taxon and counted. We used the nomenclature of Perez Farfante and Kensley (1997) for penaeid shrimps and identified species using the protocol described in Rozas and Minello (1998). Scientific and common names follow Williams et al. (1989) for other decapod crustaceans and Robins et al. (1991) for fishes. We measured total length (TL) of fishes and shrimps and carapace width (CW) of crabs.

Water depth at slack high tide was used to measure relative marsh elevation for each sample site. In a companion study (Whaley 1997), water levels were recorded every hour throughout 1995 using a permanent staff gauge and a water level recorder (WL40, Remote Data Systems, Wilmington, North Carolina) installed in Gang's Bayou (Fig. 1). Relative elevations of our sample sites on the marsh surface were determined by comparing sample water depth with the staff gauge. Elevations were then standardized to the lowest value sampled on the marsh surface (designated 0 elevation).

Density values were analyzed with analysis of variance (ANOVA) or analysis of covariance (ANCOVA) following a ln + 1 transformation required to remove the positive relationship between cell means and standard deviations in the raw data. For each sampling period, a one-way ANOVA on transformed densities of abundant taxa was used to compare location (distance from the edge) means; similar analyses were used to look for significant differ-
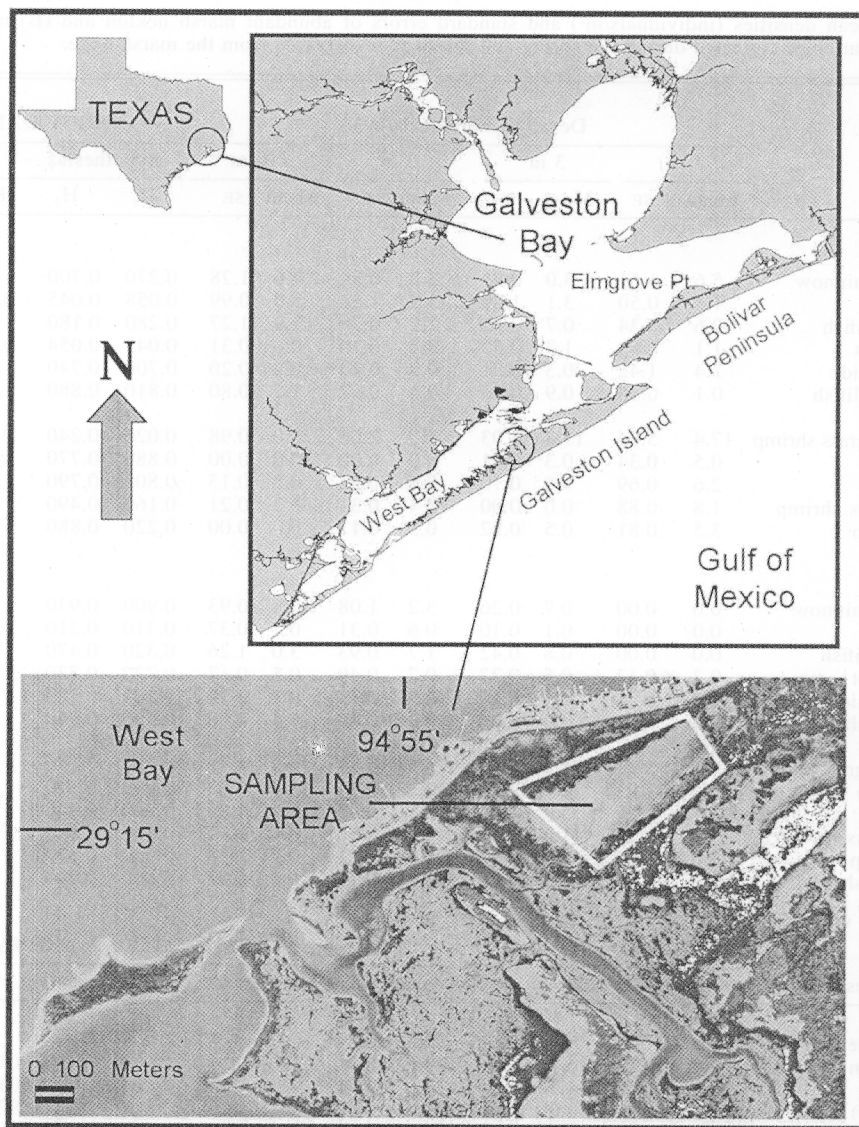
Fig. 1. Study area in Galveston Bay, Texas showing the location of Gang's Bayou and Elmgrove Point. The detailed image shows the Gang's Bayou sampling area.

ences in physical variables (untransformed) in relation to the marsh edge. When assumptions of ANCOVA (Table 1) were met, we also analyzed the density data with marsh surface elevation as a covariate. We considered probability values <0.05 to be significant.

Regression models of nekton density and distance from marsh edge

We developed regression models from the Gang's Bayou data to describe the relationships between distance from the edge and density on the marsh surface for brown shrimp, white shrimp, and blue crabs. These fishery species were relatively abundant and exhibited consistent declines in density away from the edge. We used mean values for density and the mean actual distance (measured from the center of the sampler) from the marsh edge in the models. Density data from both seasons were combined for brown shrimp and blue crabs, while only fall data were used for white shrimp. We wanted to model the pattern of density decline rather than model actual densities (which varied seasonally). Therefore, we standardized density values in the models in relation to the mean density at one meter from the edge by dividing all location means by the one meter location mean. Thus, the standardized density at one meter from the edge was 1.0 (unitless).

Validation of regression models

Predicted declines in nekton density with distance from the marsh edge were compared with independent data collected by Rozas and Zimmerman (2000) during spring and fall (1993–1994) at both mesohaline and po-

TABLE 1. (A) Mean densities (individuals/m^2) and standard errors of abundant marsh nekton and (B) mean values for environmental variables collected during the spring and fall at four distances from the marsh edge.

A) Densities

| | Density (individuals/m^2) | | | | | | | | ANCOVA/ANOVA† | | | |
| | 1 m | | 3 m | | 5 m | | 10 m | | Hypothesis‡ | | Effects | |
Taxon	Mean	SE	Mean	SE	Mean	SE	Mean	SE	H$_1$	H$_2$	Elev	Loc
Spring												
Fish												
Sheepshead minnow	5.6	1.51	3.0	0.91	2.3	0.84	4.6	1.28	0.270	0.700		0.240
Gulf killifish	1.3	0.50	3.1	1.29	3.9	1.51	3.0	0.99	0.058	0.045	0.310	0.980
Diamond killifish	0.6	0.34	0.7	0.42	1.5	0.78	2.9	1.27	0.280	0.180		0.280
Striped mullet	1.1	0.59	1.3	0.50	0.1	0.10	0.6	0.31	0.045	0.054	0.150	0.270
Inland silverside	3.4	1.42	0.3	0.21	0.2	0.20	0.2	0.20	0.700	0.740		0.006
Rainwater killifish	0.1	0.10	0.9	0.53	0.4	0.22	1.2	0.80	0.810	0.880		0.570
Crustacean												
Daggerblade grass shrimp	17.4	5.84	11.3	3.03	8.7	2.03	3.0	0.98	0.026	0.240	0.008	0.019
White shrimp	0.5	0.34	0.3	0.21	0.0	0.00	0.0	0.00	0.880	0.770		0.233
Blue crab	2.6	0.69	1.8	0.70	0.6	0.22	0.2	0.13	0.800	0.790		0.001
Brackish grass shrimp	1.8	0.88	0.0	0.00	0.4	0.31	0.3	0.21	0.160	0.490		0.078
Brown shrimp	3.5	0.81	0.5	0.22	0.5	0.17	0.0	0.00	0.220	0.880		<0.001
Fall												
Fish												
Sheepshead minnow	0.0	0.00	0.7	0.26	3.2	1.08	2.8	0.93	0.900	0.930		<0.001
Bulf killifish	0.0	0.00	0.1	0.10	0.6	0.31	0.7	0.37	0.310	0.210		0.105
Diamond killifish	0.0	0.00	0.8	0.42	1.7	0.93	3.0	1.26	0.320	0.470		0.019
Striped mullet	0.2	0.13	0.5	0.27	0.7	0.40	0.5	0.17	0.720	0.730		0.633
Inland silverside	0.3	0.21	0.1	0.10	0.3	0.15	0.1	0.10	0.290	0.380		0.627
Rainwater killifish	0.0	0.00	0.0	0.00	0.1	0.10	1.1	0.50	0.990	0.990		0.003
Crustacean												
Daggerblade grass shrimp	8.1	3.11	14.7	2.61	24.7	4.12	16.5	4.78	0.130	0.076		0.001
White shrimp	39.5	11.91	8.4	2.57	2.2	0.74	1.7	0.65	0.093	0.170		0.001
Blue crab	8.1	2.29	5.9	2.06	3.1	0.46	2.9	0.85	0.840	0.740		0.122
Brackish grass shrimp	1.9	1.17	1.6	0.56	2.2	0.66	0.4	0.31	0.800	0.840		0.127
Brown shrimp	0.6	0.31	0.6	0.40	0.3	0.21	0.2	0.13	0.650	0.870		0.741
Marsh grass shrimp	4.3	4.30	0.2	0.20	0.1	0.10	0.0	0.00	0.600	0.740		0.566

B) Environmental variables

| | 1 m | | 3 m | | 5 m | | 10 m | | ANOVA† |
Variables	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Location effect
Spring									
Distance to edge (m)	1.0	0.06	3.4	0.17	5.1	0.14	9.7	0.23	
Water depth (cm)	24.4	2.10	16.1	1.53	13.6	0.91	13.8	1.44	0.001
Elevation (cm)	16.4	2.14	24.7	1.41	27.0	0.91	26.8	0.88	0.001
Temperature (C)	29.8	0.80	30.0	0.88	30.0	0.97	30.2	0.90	0.992
Salinity (psu)	12.5	0.64	12.0	0.65	12.3	0.75	11.5	0.60	0.73
Turbidity (FTU)	16.1	2.61	27.2	5.58	43.2	11.25	26.4	5.71	0.072
Dissolved oxygen (μL/L)	9.8	0.53	8.3	1.03	8.1	0.70	6.4	0.49	0.036
Fall									
Distance to edge (m)	1.3	0.10	3.7	0.18	5.6	0.24	11.2	0.24	
Water depth (cm)	52.1	1.60	44.7	1.85	42.1	0.77	44.6	1.49	0.000
Elevation (cm)	17.0	1.64	24.7	1.79	27.3	0.85	24.9	1.43	0.000
Temperature (C)	24.3	0.43	24.4	0.44	24.3	0.47	24.5	0.37	0.986
Salinity (psu)	20.8	0.33	20.8	0.33	20.8	0.33	20.8	0.33	1.0
Turbidity (FTU)	7.0	1.38	5.9	1.05	6.1	1.07	7.7	1.29	0.700
Dissolved oxygen (μL/L)	4.4	0.32	4.5	0.36	4.2	0.34	3.8	0.29	0.401

Notes: The P value shown for the Location (Loc) effect is from a one-way ANOVA comparing the four location means. The P value for the Elevation (Elev) effect is only shown if one of the preliminary assumptions of ANCOVA was met.

† Values presented for ANCOVA/ANOVA results are P values.

‡ Null hypothesis tested: H$_1$, $\beta = 0$; H$_2$, $\beta1 = \beta3 = \beta5 = \beta10$.

lyhaline marshes in the Galveston Bay system. They measured densities at 0.5–2 m and 5–10 m from the marsh edge at randomly selected locations in these different marsh systems. For seven of their location/season combinations, we calculated mean densities (between 4 and 8 samples per mean) and distances from the marsh edge, calculated the actual decrease in mean density from the edge to the inner marsh samples, and compared these results with predicted decreases in density based on our standardized regression models developed from the Gang's Bayou data. We used paired t tests to compare actual and predicted declines in density.
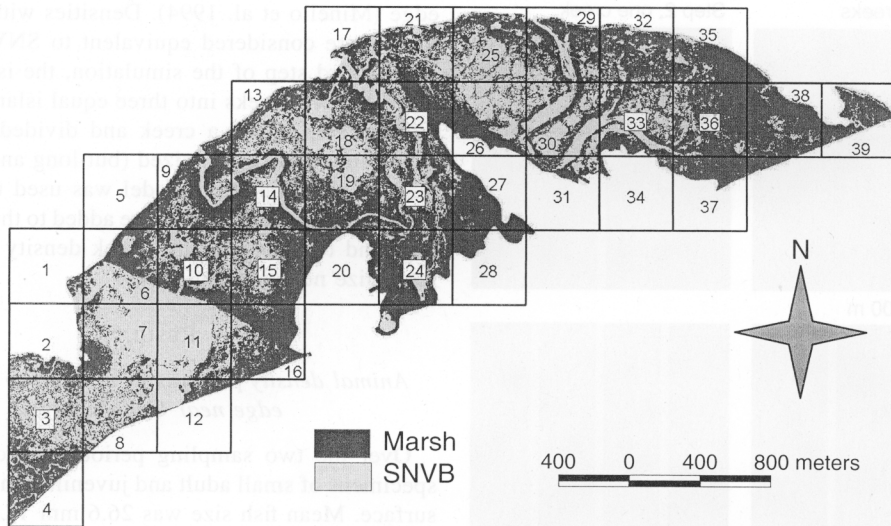
Fig. 2. The marsh complex at Elmgrove Point on Bolivar Peninsula in the Galveston Bay system. The numbered grid shows the 39 16-ha sectors used to examine relationships between marsh–water spatial configuration and nekton populations. SNVB is shallow nonvegetated bottom.

Estimating animal populations in a natural marsh

We estimated nekton populations at Elmgrove Point in the Galveston Bay system (Figs. 1 and 2). This polyhaline marsh complex (total of 437 ha) located on the bayside of Bolivar Peninsula was one of the areas sampled by Rozas and Zimmerman (2000) and used in the validation of our regression models. Populations for brown shrimp, white shrimp, and blue crabs were estimated using our standardized density models, summary density data from Texas and Louisiana, and a Geographic Information System (GIS) analysis of the marsh–water spatial configuration. The summary density data were obtained from Minello (1999) for polyhaline marsh edge and shallow nonvegetated bottom (SNVB); these data were based exclusively on enclosure samples and should provide accurate density estimates (Rozas and Minello 1997). Specifically, densities used for vegetation at 1 m from the marsh edge were 10.4 individuals/m^2 for brown shrimp, 10.3 individuals/m^2 for white shrimp, and 6.1 individuals/m^2 for blue crab. For SNVB, densities were 2.5 individuals/m^2 for brown shrimp, 2.2 individuals/m^2 for white shrimp, and 1.0 individuals/m^2 for blue crab. These density estimates are for seasons when the species are relatively abundant in marshes of Texas and Louisiana: spring through fall for brown shrimp, summer and fall for white shrimp, and year around for blue crabs (Minello 1999).

Within the marsh complex, the area of SNVB and the areas of vegetation at different distances from the marsh edge were calculated using ArcView 3.1 with Image Analyst and Spatial Analyst extensions and the Data Automation Kit (Environmental Systems Research Institute, Redlands, California). We used a 1-m ground resolution Digital Orthophoto Quarter Quad-rangle (DOQQ) image analyzed by the United States Geological Survey from a color-infrared aerial photograph (1:40 000 scale) taken 5 February 1995; the DOQQ was overlaid and displayed on a National Wetland Inventory (NWI) digital map developed by the United States Fish and Wildlife Service (after conversion from NAD27 to NAD83). The overall area of the DOQQ that was classified as regularly flooded emergent marsh and nonvegetated unconsolidated bottom on the NWI map was clipped and classified into 25 categories using the Iterative Self-Organizing Data Analysis technique in Image Analyst. These categories were then assigned to either vegetated marsh or SNVB by examining the image, consulting experts familiar with the area, and conducting limited ground truthing. Within vegetated areas, the distance from SNVB was calculated using Spatial Analyst. The overall areal coverage within the vegetation was then calculated for different distances from the marsh edge (e.g., for 0–1 m, 1–2 m, and so on). Modeled densities were then applied for each area to estimate nekton populations for the entire marsh complex.

Marsh vegetation at Elmgrove point is thought to have originally developed on a washover fan, where sediment from the Gulf of Mexico washed over Bolivar Peninsula during a major storm event. A 1932 aerial photograph of the area shows marsh vegetation that was relatively solid and unfragmented. Commercial development on Bolivar Peninsula has restricted additional input of Gulf of Mexico sediments through washover events, subsidence rates for the peninsula have been relatively high (between 0.5 and 1.0 cm/yr between 1943 and 1973, Gabrysch and Coplin 1990), and a fault line is apparent in the western portion of the marsh complex (see sectors 6, 10, and 16; Fig. 2). These
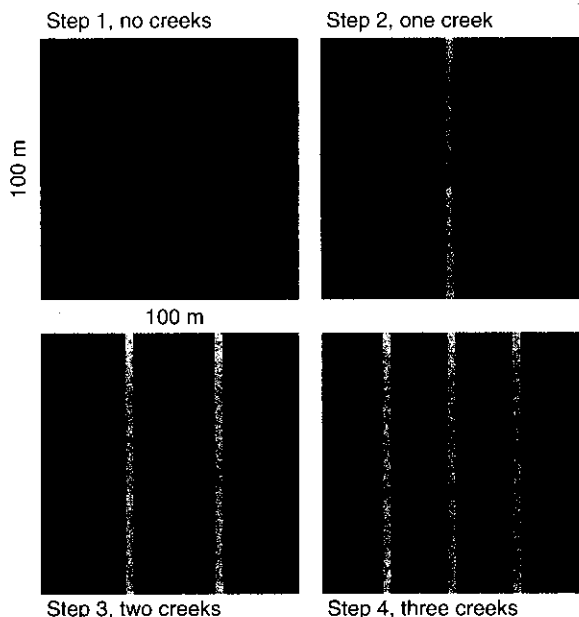
Step 1, no creeks   Step 2, one creek

100 m

100 m

Step 3, two creeks   Step 4, three creeks

FIG. 3. Marsh–water configurations as creeks are added to a simulated created marsh. The first four simulation steps are shown with 0–3 creeks in the marsh. Each creek was 2 m wide.

conditions suggest that the marsh complex is degrading and fragmenting at various rates due to sediment deprivation and differential subsidence. To examine spatial variability in population estimates and relationships between nekton and marsh fragmentation, we overlaid a grid of 39 equal sectors (~16 ha each) over 429 ha of the marsh image (the amount of marsh complex in the sectors ranged from 1 to 16 ha). Nekton population estimates, the percentage of open water, and the amount of edge were determined for each sector. Image resolution is an important factor in quantifying edge; we calculated edge by summing the number of 1-m marsh pixels adjacent to water (reported as linear meters per hectare).

Simulation model for created salt marshes

We also examined the effect of adding edge to created salt marshes by calculating nekton populations for a simulated square 1-ha marsh island. In the initial step of the simulation, the island is solid marsh vegetation, and densities of brown shrimp, white shrimp, and blue crabs decline from the periphery of the island following our modeled relationships based on the same summary density data used in the Elmgrove Point analysis (Minello 1999). Nekton densities for the marsh complex were calculated at a 1-m pixel resolution, and population size was determined by summing results from the 10 000 pixels. In the second step of the simulation, we bisected the island with a straight 2-m wide marsh creek (Fig. 3) and recalculated the nekton population size assuming that vegetation along the newly added creek had high nekton densities associated with marsh

edge (Minello et al. 1994). Densities within the creek itself were considered equivalent to SNVB densities. In the third step of the simulation, the island was divided by two creeks into three equal islands. Each additional step added a creek and divided the original island into more equal-sized (but long and narrow) islands. This simulation model was used to track population changes as creeks were added to the marsh complex and to determine the creek density necessary to maximize nekton populations.

RESULTS

Animal density patterns in relation to the marsh edge near Gang's Bayou

Over the two sampling periods, we collected 733 specimens of small adult and juvenile fish on the marsh surface. Mean fish size was 26.6 mm TL (SE = 0.87), the range was 4–330 mm, and 97% of the specimens were under 100 mm. The dominant species were the sheepshead minnow *Cyprinodon variegatus*, gulf killifish *Fundulus grandis*, diamond killifish *Adinia xenica*, striped mullet *Mugil cephalus*, inland silverside *Menidia beryllina*, and the rainwater killifish *Lucania parva*. In the spring, only the inland silverside exhibited significant location effects in the marsh with mean densities being highest near the marsh edge (Table 1). In the fall, the sheepshead minnow, diamond killifish, and rainwater killifish all had significantly higher densities at the inner marsh locations. A total of 21 species of fish were collected during the two seasons sampled, and less abundant species (with overall mean density in fish/m^2 [±1 SE]) included bayou killifish *Fundulus pulvereus* (0.34 ± 0.105), saltmarsh topminnow *Fundulus jenkinsi* (0.18 ± 0.105), code goby *Gobiosoma robustum* (0.13 ± 0.067), western mosquitofish *Gambusia affinis* (0.11 ± 0.078), pinfish *Lagodon rhomboides* (0.09 ± 0.036), sailfin molly *Poecilia latipinna* (0.09 ± 0.054), spotted seatrout *Cynoscion nebulosus* (0.08 ± 0.039), longnose killifish *Fundulus similis* (0.05 ± 0.030), and darter goby *Gobionellus boleosoma* (0.05 ± 0.030). Fish species diversity (the number of species identified in 20 m^2 of marsh surface over the two sampling periods) was similar among the sampling locations, with 13, 14, 14, and 12 species collected at the 1-, 3-, 5-, and 10-m locations, respectively.

We also collected 2076 specimens of natant decapod crustaceans; mean size was 22.8 mm TL (SE = 0.34), the range was 2–90 mm, and 92% of the specimens were under 50 mm. The daggerblade grass shrimp *Palaemonetes pugio* was most abundant followed by white shrimp, blue crab, brackish grass shrimp *Palaemonetes intermedius*, brown shrimp, and marsh grass shrimp *Palaemonetes vulgaris*. Densities of daggerblade grass shrimp were significantly affected by location in the marsh, but patterns were inconsistent from one season to the next. In spring, the highest mean density of this species, and its congener the brackish
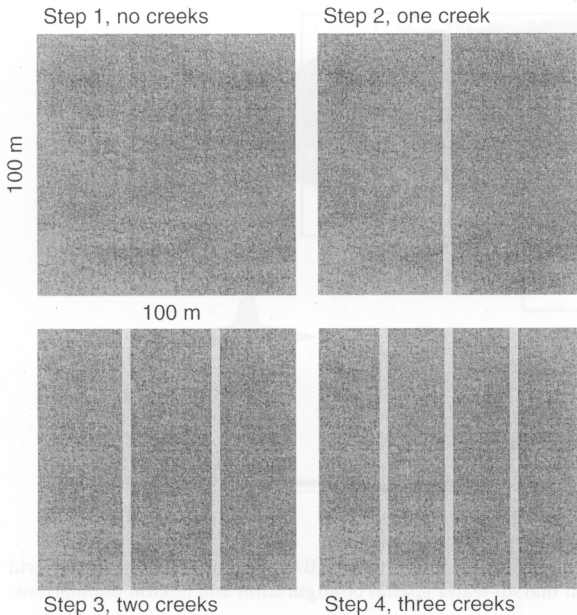
Fig. 3. Marsh–water configurations as creeks are added to a simulated created marsh. The first four simulation steps are shown with 0–3 creeks in the marsh. Each creek was 2 m wide.

grass shrimp, was found at one meter from the edge, and densities declined with distance from the marsh edge (Table 1). In fall, however, the highest mean densities occurred at the 5- and 10-m locations. Blue crab and brown shrimp densities declined significantly with distance from the marsh edge in the spring; similar patterns were apparent in the fall, although the ANOVA results were not statistically significant. White shrimp were only abundant in fall, and densities of this species declined rapidly with distance from the marsh edge.

The focus of our marsh sampling was on nekton, but we also collected other benthic, epibenthic, and epifaunal organisms in the drop samples. The most abundant of these was the fiddler crab (*Uca* spp.) and marsh periwinkle (*Littoraria irrorata*). The overall mean density of fiddler crabs was 8.3/m² (SE = 1.93), and densities were highest away from the marsh edge. Marsh periwinkles were found mainly on *Spartina* stems, overall density was 9.4 snails/m² (SE = 1.51), and there were no significant density differences in relation to the marsh edge. We also collected low densities (all means <0.4 animals/m²) of the heavy marsh crab *Sesarma reticulatum*, squareback marsh crab *Sesarma cinereum*, thinstripe hermit *Clibanarius vittatus*, bigclaw snapping shrimp *Alpheus heterochaelis*, Atlantic mud crab *Panopeus herbstii*, gulf grassflat crab *Dyspanopeus texana*, and surf hermit crab *Isocheles wurdemanni*. Species diversity (measured as for fish) of all decapod crustaceans was lowest at the 10-m location, with 13, 12, 13, and 9 species collected at the 1-, 3-, 5-, and 10-m locations, respectively.

Water temperature, salinity, and turbidity did not vary significantly in relation to the marsh edge (Table 1). Dissolved oxygen varied among sampling locations in the spring, but the lowest mean values (at 10 m from the edge) were still above 6 μL/L and unlikely to affect animal distributions. Overall mean salinity was higher in the fall than in the spring (fall, 20.8 ± 0.16 psu; spring, 12.1 ± 0.32 psu [means ± 1 SE], while mean temperature (fall, 24.3 ± 0.20°C; spring, 30.0 ± 0.43°C [means ± 1 SE] and turbidity (fall, 6.7 ± 0.59 FTU; spring, 28.2 ± 3.71 FTU [means ± 1 SE]) were lower in the fall. The tide was relatively high during the fall sampling period, and overall mean water depth was substantially higher in the fall (45.9 cm, SE = 0.93) than in the spring (17.0 cm, SE = 1.03). As in many marshes of lower Galveston Bay (Minello et al. 1991, Minello and Webb 1997), there was little if any berm present, and elevations consistently increased with distance from the edge (Table 1).

Marsh surface elevation and nekton density

We used analysis of covariance (ANCOVA) to determine whether the observed nekton distributions were more closely related to distance from the edge (location effect) or to elevation of the marsh surface. Elevation was the covariate in this analysis. In most cases, the assumptions of ANCOVA requiring that both a signif-
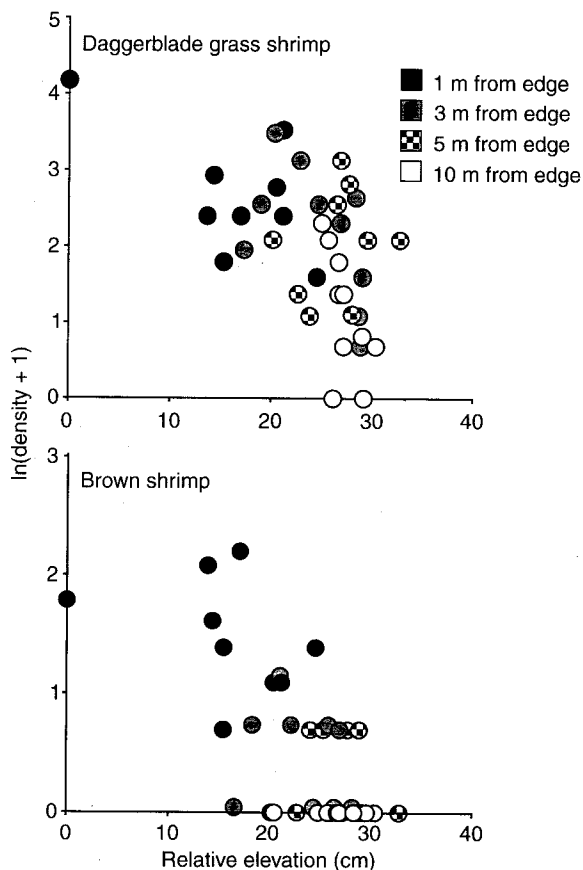

FIG. 4. Examples of relationships between densities (animals/m²; daggerblade grass shrimp and brown shrimp) and elevation of the marsh surface at the Gang's Bayou marsh in spring 1995. For most species (like brown shrimp), elevation was not significantly related to density.

icant density/elevation relationship (i.e., rejecting the null hypothesis that $\beta = 0$) or that density/elevation slopes were similar at the different sampling locations (i.e., accepting the null hypothesis that $\beta_1 = \beta_3 = \beta_5 = \beta_{10}$) were not met (Table 1). Overall, the analysis indicated that elevation generally did not explain a significant amount of variability in spatial patterns of nekton density on the marsh surface. We also examined scatter plots and found little evidence for nonlinear relationships between log-transformed densities and elevation (Fig. 4). In only one instance, was elevation significant in the ANCOVA; in spring, densities of daggerblade grass shrimp decreased with increasing elevation on the marsh surface (Fig. 4). In this analysis, the location effect was still significant after the elevation effect was removed.

Regression models of nekton density and distance from marsh edge

For brown shrimp and white shrimp, we used exponential curves to model the decline of standardized densities on the marsh surface with distance from the
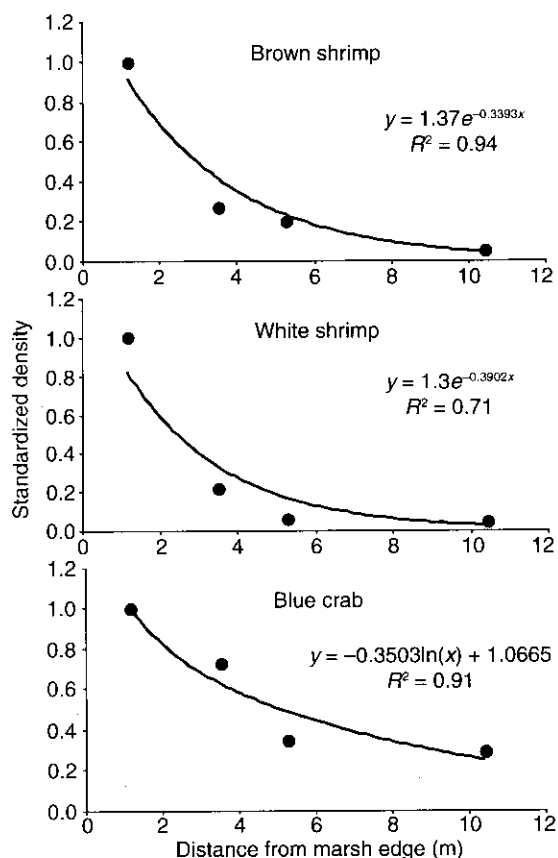
FIG. 5. Regression models describing density patterns in relation to the marsh edge at Gang's Bayou. Points represent standardized mean densities from spring and fall for brown shrimp and blue crabs and from fall for white shrimp. Densities are standardized in relation to mean values at 1 m from the edge; thus the value at this distance is 1.0 (unitless). The y-intercept was set at 1.37 for brown shrimp and 1.30 for white shrimp $(1.0 + 1$ SE$)$.

edge (Fig. 5). We set the y-intercept at 1.37 for brown shrimp and 1.30 for white shrimp $(1.0 + 1$ SE$)$. The model R^2 was 0.94 for brown shrimp and 0.71 for white shrimp. The blue crab data were modeled with a logarithmic relationship, and the R^2 for this model was 0.91 (Fig. 5). We truncated the blue crab model so that densities never became negative; at distances above 21 m from the edge, densities equaled zero.

Validation of regression models

Modeled density declines in relation to marsh edge were generally similar to patterns measured independently by Rozas and Zimmerman (2000) in two different marsh systems of Galveston Bay. For brown shrimp and blue crabs, the mean distance from the marsh edge in the seven validation data sets ranged from 0.5 to 1.2 m for the edge samples and 5.7 to 7.4 m for inner marsh samples (Table 2). For brown shrimp, actual density declines ranged from 76.2% to 100%, and a comparison of modeled declines and actual de-

clines indicated that the mean difference was not significantly different from zero (paired t test, $P = 0.63$). The differences between actual density declines and predicted declines for blue crabs were more variable, although the mean difference was only 1.2% and not significantly different from zero (paired t test, $P = 0.92$). The validation data set for white shrimp was small, because only fall data were used. The model consistently overestimated the actual density declines for this species. Results from the paired t test were not significant $(P = 0.10)$ at the 5% level, but with only three pairs, the power of this analysis was low. The fit between actual and predicted densities in the inner marsh was poorest for the Elmgrove Point validation data (Table 2). Because of these results, we modified the white shrimp model by including the three validation means in the analysis. The resulting model: density $= 1.3\ e^{-0.3174\ (\text{DISTANCE})}$ had an R^2 of 0.48.

Nekton populations at Elmgrove Point

The highly fragmented salt marsh complex at Elmgrove Point (Fig. 2) had a total area of 437 ha; 37.4% of the area was shallow nonvegetated bottom (SNVB). The remaining 62.6% of the area was salt marsh vegetation (mainly *Spartina alterniflora*), with 9.5% of the total area (>15% of the vegetated area) being vegetation within 1 m of the marsh–water interface. For each 1-m increment away from the edge, the area covered decreased; 46.2% of the overall area (73.8% of the vegetated area) was within 10 m of the marsh edge (Table 3). When we applied our predicted nekton densities to the areal coverage values from the GIS analysis, we estimated overall populations in the 437-ha marsh complex at 16.2 million brown shrimp (37 000 shrimp/ha), 15.5 million white shrimp (35 000 shrimp/ha), and 11.3 million blue crabs (26 000 crabs/ha).

Population estimates in the 39 sectors of marsh, however, were quite variable because the sectors had different configurations of marsh vegetation and SNVB. Sector estimates ranged from 1000 to 50 300 shrimp/ha for brown shrimp, 1100 to 47 200 shrimp/ha for white shrimp, and 1400 to 33 600 crabs/ha for blue crabs. There was a direct positive relationship between the amount of edge per hectare in a sector and the population size, as should be expected because these species are concentrated in this edge habitat. The amount of edge in sectors was positively related to the percentage of SNVB up to ~20–25%; at higher levels of SNVB, the amount of edge was variable (Fig. 6). Nekton population estimates also increased in size with the percentage of SNVB in a sector up to ~20–25% (Fig. 7); at higher levels of SNVB, population estimates were relatively stable and only appeared to decline when SNVB reached 70–80%. Populations at 100% SNVB (based on the mean densities used for this habitat type) were projected to be 25 000 shrimp/ha for brown shrimp, 22 000 shrimp/ha for white shrimp, and 10 000 crab/ha for blue crab (Fig. 7).

TABLE 2. Comparison of actual and predicted declines in nekton density with distance away from the marsh edge.

Season/Year	Location	Edge		Inner		Actual decline (%)	Predicted decline (%)	Difference (actual − predicted, %)
		Density (no./m^2)	Distance (m)	Density (no/m^2)	Distance (m)			
Brown shrimp								
Spring 1994	Elmgrove East	27.4	0.7	1.8	6.9	93.4	87.8	5.6
Spring 1994	Elmgrove West	22.0	0.5	5.0	7.1	77.3	89.3	−12.1
Fall 1994	Elmgrove East	4.2	1.2	1.0	6.7	76.2	84.5	−8.3
Fall 1994	Elmgrove West	2.4	1.2	0.2	5.7	91.7	78.3	13.4
Spring 1993	Atkinson Island	16.3	0.6	0.7	7.4	95.9	90.0	5.8
Spring 1993	Hog Island	1.3	0.7	0.0	7.2	100.0	89.0	11.0
Fall 1993	Atkinson/Hog Island	2.3	0.7	0.4	6.4	83.1	85.5	−2.4
Mean difference								1.9
Blue crabs								
Spring 1994	Elmgrove East	3.8	0.7	0.2	6.9	94.7	67.3	27.5
Spring 1994	Elmgrove West	1.8	0.5	1.2	7.1	33.3	71.0	−37.7
Fall 1994	Elmgrove East	11.6	1.2	1.2	6.7	89.7	60.1	29.6
Fall 1994	Elmgrove West	4.2	1.2	2.0	5.7	52.4	54.4	−2.1
Spring 1993	Atkinson Island	3.5	0.6	0.5	7.4	85.7	70.7	15.1
Spring 1993	Hog Island	1.3	0.7	1.0	7.2	20.0	68.5	−48.5
Fall 1993	Atkinson/Hog Island	7.3	0.7	0.8	6.4	89.7	65.1	24.6
Mean difference								1.2
White Shrimp								
Fall 1994	Elmgrove East	20.6	1.2	8.2	6.7	60.2	88.3	−28.1
Fall 1994	Elmgrove West	19.4	1.2	11.6	5.7	40.2	82.7	−42.5
Fall 1993	Atkinson/Hog Island	13.5	0.7	2.9	6.4	78.7	89.2	−10.5
Mean difference								−27.0

Notes: The mean densities and distances from the marsh edge are based on data collected by Rozas and Zimmerman (2000) at Elmgrove Point and in upper Glaveston Bay (Atkinson Island and Hog Island). Predicted declines were calculated from regressions developed from Gang's Bayou data.

TABLE 3. Results of GIS analysis at the 437-ha Elmgrove Point marsh complex showing the percentage of the area that is composed of shallow nonvegetated bottom (SNVB) and marsh at different distances from the edge.

Micro-habitat (m)	Total area (%)	Brown shrimp density (no./m^2)	Pop-ulation (%)
SNVB	37.4	2.50	25.1
0–1	9.5	12.07	30.9
1–2	7.4	8.60	17.2
2–3	7.3	6.12	12.0
3–4	5.0	4.36	5.8
4–5	4.9	3.11	4.1
5–6	3.1	2.21	1.9
6–7	2.6	1.52	1.0
7–8	2.5	1.12	0.8
8–9	2.1	0.80	0.5
9–10	1.8	0.57	0.3
10–11	1.3	0.41	0.1
11–12	1.1	0.29	0.1
12–13	1.2	0.21	0.1
13–14	0.9	0.15	0.0
14–15	0.9	0.10	0.0
15–16	0.6	0.07	0.0
16–17	0.7	0.05	0.0
17–18	0.6	0.04	0.0
18–19	0.5	0.03	0.0
19–20	0.5	0.02	0.0
20–21	0.4	0.01	0.0
21–22	0.4	0.01	0.0
>22	7.2	0.01	0.0

Note: As an example, the modeled densities for brown shrimp are also shown for each microhabitat along with the percentage of the estimated brown shrimp population (16.2 × 10^6) associated with that microhabitat.

Simulation model for created salt marshes

Shrimp populations in the simulated 1-ha created marsh increased rapidly from ~16 000 shrimp/ha for a solid vegetated island without creeks to ~70 000 shrimp/ha in a marsh complex with 10 creeks (Fig. 8). These 10 creeks divided the original marsh island into 11 narrow islands (each 7.3 m in width), and the marsh complex was 20% creek bottom or SNVB. The initial modeled population of 16 000 blue crabs with no creeks in the marsh increased to 46 000 blue crabs after 8 creeks were added; the islands at this step of the model were 9.3-m wide and 16% of the area was SNVB. As more creeks were added, the model populations increased slowly, reaching maximum values per hectare
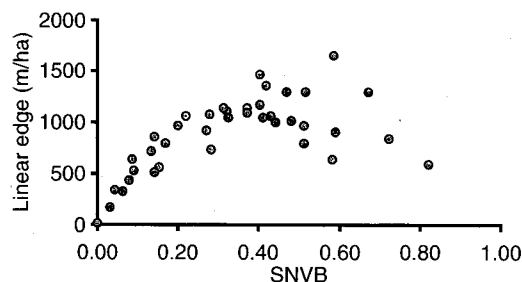

FIG. 6. The relationship between the percentage of open water or shallow nonvegetated bottom (SNVB) and the amount of linear edge (in meters per hectare) for the 39 sectors analyzed at Elmgrove Point.
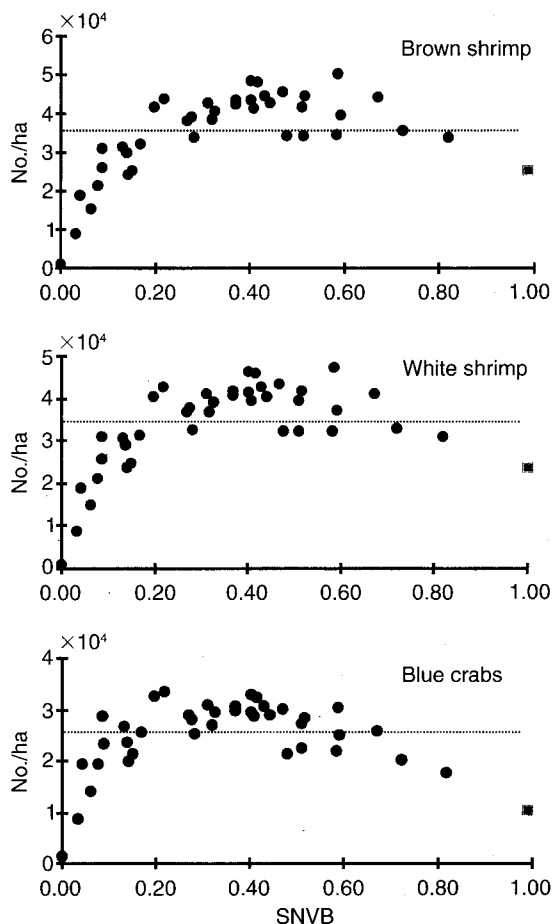
FIG. 7. Relationships between the percentage of open water or shallow nonvegetated bottom (SNVB) and the population estimates (animals per hectare) for brown shrimp, white shrimp, and blue crabs in the 39 sectors analyzed at Elmgrove Point. The horizontal dotted line represents the overall population estimate for the entire marsh complex. The shaded square at 100% SNVB was not generated from the 39 sectors, but represents the estimated population based on the mean density for SNVB used in the models.

of 78 500 brown shrimp, 74 400 white shrimp, and 49 500 blue crabs when 16 creeks were added (32% SNVB).

DISCUSSION

Juvenile brown shrimp, white shrimp, and blue crabs are temporary residents of coastal marsh systems in the northwestern Gulf of Mexico, and they are closely associated with vegetation at the marsh edge (Zimmerman et al. 1984, Zimmerman and Minello 1984, Peterson and Turner 1994, Rozas and Minello 1998, Minello 1999). Zimmerman et al. (2000) reviewed the substantial evidence for linkages between salt marshes and productivity of these nekton species, and there is some correlative evidence relating the amount of marsh edge to shrimp productivity (Faller 1979, Browder et al. 1989). At Gang's Bayou, densities of these three

crustacean species on the marsh surface were highest 1 m from the water's edge, and they declined rapidly to 10 m. Our regression models developed to describe these fine-scale density patterns were tested with independent data and appeared to adequately predict density declines in other marsh systems of Galveston Bay. We focused our modeling efforts and additional analyses on these species because of their fine-scale spatial distribution, commercial importance, relatively high abundance, and dependence on salt marshes.

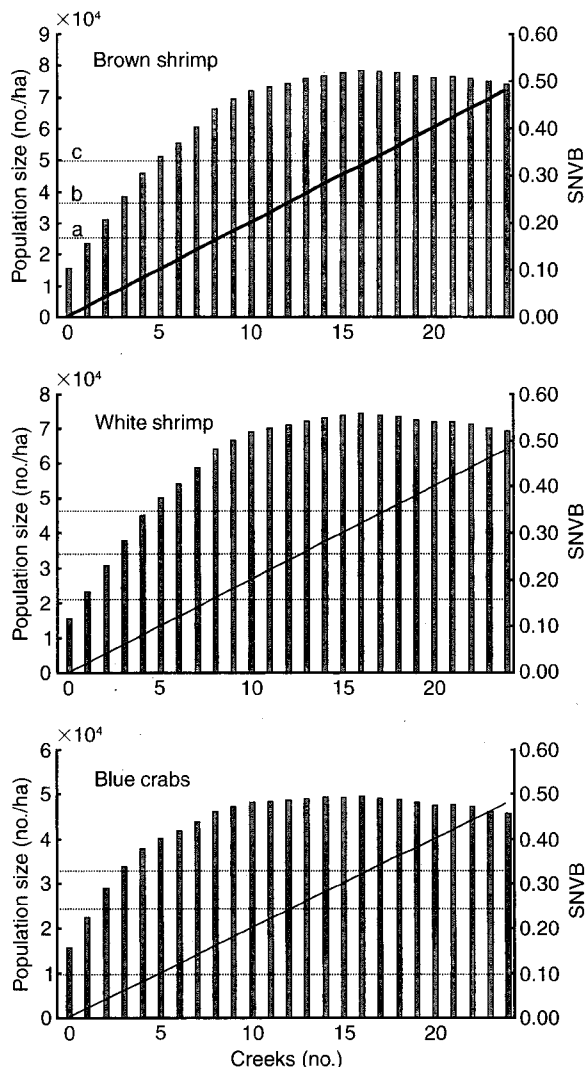Most other abundant nekton species found on the

FIG. 8. Simulation results showing the relationships between creek density and population size in a 1-ha created marsh island. The solid diagonal line shows the percentage of shallow nonvegetated bottom (SNVB; equivalent to creek bottom) within the marsh complex. The horizontal dotted lines represent three target population sizes: (a) lower, population size if the entire 1-ha area was SNVB, (b) middle, overall population for the Elmgrove Point complex, and (c) upper, maximum population estimated from the 39 cells at Elmgrove Point.

marsh surface were not consistently associated with the marsh edge. The dominant nekton species in the Gang's Bayou marsh was the daggerblade grass shrimp, and this resident has been associated with edge habitat in other studies where spatial resolution was relatively low (Peterson and Turner 1994, Minello 1999). Densities of this species were highest at the 1-m location in our spring samples, but mean densities in fall were highest at 5 m from the edge. Tidal flooding was more extensive during the fall sampling period, and this apparent distribution shift may have been related to water depth or extent of tidal inundation. Most resident marsh fishes did not exhibit consistently high densities near the marsh edge, and some fish species such as the sheepshead minnow, diamond killifish, and rainwater killifish had significantly higher densities at our inner marsh sampling locations.

Distance to the edge and elevation of the marsh surface are related, and in many Galveston Bay marshes, which have minimal berms, elevation increases coincident with distance from the edge. Both of these factors have been identified as important in determining use of the vegetated marsh surface by nekton (Kneib and Wagner 1994, Minello et al. 1994, Minello and Webb 1997, Rozas and Zimmerman 2000). Our results from Gang's Bayou suggest that over some broad range of slopes in *Spartina alterniflora* marshes of Galveston Bay, distance from the edge can be used to predict nekton density (at least for penaeid shrimps and blue crabs) in the inner marsh, regardless of elevation. However, some of the variability in our model validation tests, using density data from different areas of the bay, can likely be attributed to elevation and slope differences in the marshes. In other types of marshes (e.g., *S. patens* or *Juncus*), elevational range would have been greater, and elevation may have been more important.

We combined fine-scale density relationships with landscape-scale patterns of marsh and water to estimate population sizes for juvenile brown shrimp (16.2 million), white shrimp (15.5 million), and blue crabs (11.3 million) in the 437-ha marsh complex at Elmgrove Point. The size of these populations helps explain why coastal wetlands are considered valuable nurseries. We believe that these population estimates are representative of many coastal marsh systems in the northwestern Gulf of Mexico. However, the estimates are based on many assumptions, and errors can originate from a number of sources. We used average densities in the models for polyhaline edge marsh and shallow nonvegetated bottom (SNVB) taken from 22 studies in coastal areas of Texas and Louisiana (Minello 1999). This approach is useful in examining landscape patterns and providing average population estimates, but actual densities and populations will vary for any particular time and place; and in some cases this variability will be substantial (Rozas 1993, McIvor and Rozas 1996, Kneib 1997a). Geographic-scale differences in density related to salinity regimes is an obvious factor

that should be considered in any attempt to use the models at other locations (Clark et al. 1999, Minello 1999). The pattern of density decline with distance away from the marsh edge also varies as can be seen in our validation data (Table 2). As discussed above, we would expect this pattern to be affected by large differences in marsh slope, but there may be other important factors as well. Because young shrimp and crabs recruit into the marshes from the Gulf of Mexico, tidal connectivity can also affect marsh use (Rey et al. 1990, Rogers et al. 1994, Rozas and Minello 1999). In our population estimates, we have assumed complete connectivity between SNVB and the open bay. This assumption is reasonable at Elmgrove Point because marsh elevations are relatively low in the tidal frame (evidenced by the dominance of *S. alterniflora*) and there are many tidal creeks and ponds. However, in high-marsh systems with few creeks, and certainly in impounded areas influenced by structural marsh management, the extent of tidal connectivity is likely to be an important issue that would affect population estimates. There is also error related to the GIS estimates of marsh and water coverages that is caused by resolution limitations and classification errors. Despite these many caveats, we believe that this modeling approach is useful in estimating population sizes in polyhaline, regularly flooded, tidal marshes of the Galveston Bay system. With certain adjustments and calibrations, the approach could also be applicable to other marsh systems in the northwestern Gulf of Mexico.

Most of the shrimp and blue crabs in the Elmgrove Point marsh complex were within marsh vegetation at flood tide (our estimates were 74.9% of the brown shrimp population, 76.8% of white shrimp, and 85.5% of blue crabs), and densities declined steeply with distance from the marsh edge; thus, we focused our population modeling exercise on fine-scale distribution patterns over the marsh surface. We assigned a single mean density to all SNVB, but there is also some evidence for a nekton density gradient away from the marsh edge into shallow open water (Baltz et al. 1993, Rozas and Zimmerman 2000). In future refinements of this modeling approach (especially when estimating populations of nekton that do not strongly select for vegetation), density decline models should be developed for the edge of marsh ponds and other estuarine water bodies. In addition, although there was little evidence for submerged aquatic vegetation (SAV) at Elmgrove Point, the presence of SAV can dramatically increase densities of decapod crustaceans and some fishes in shallow estuarine waters (Weaver and Holloway 1974, Heck and Orth 1980, Duffy and Baltz 1998, Rozas and Minello 1998, 1999, Castellanos and Rozas 2001) and must be considered in estimating population sizes of these species.

Fundamental differences in the use of salt marshes by transient nekton probably preclude the application of these particular models to marsh systems on the

Atlantic and Pacific coasts of the United States. These marshes differ in densities of nekton on the marsh surface, landscape patterns and the amount of marsh edge, tidal regimes and inundation levels, and topography and elevational ranges (Kneib 1994, 1997a, Rozas 1993, 1995, McIvor and Rozas 1996, Zedler et al. 1999, Desmond et al. 2000, Kneib 2000, Zimmerman et al. 2000). However, the approach of combining fine-scale distributions and landscape-scale patterns should still be useful in estimating populations and examining ecological processes in these marsh systems (Kneib 1994).

Our modeling approach allowed us to examine how landscape patterns can affect nekton populations. Browder et al. (1985, 1989) developed a model of marsh disintegration that suggested marshes reach a maximum amount of edge when they are ~50% water and the fishery value of the marsh is maximized at this marsh–water configuration. Our analysis of the fragmented marsh complex at Elmgrove Point (which we believe is a slowly disintegrating marsh complex) allowed us to examine this marsh disintegration model in more detail with respect to shrimp and blue crabs; the 1-m ground resolution of our GIS analysis provides a more appropriate spatial scale for analyzing nekton use patterns. The amount of edge in a sector at Elmgrove Point increased consistently with the percentage of SNVB until reaching 20–25% (Fig. 6). Above that level, however, the relationship was quite variable. Similarly, the estimated nekton populations in each cell increased steeply until the cell contained ~20% SNVB, and then populations leveled out. The maximum % SNVB measured in the 39 sectors was just over 80%, and population declines were not apparent until the SNVB was over 70%. These modeled population estimates will not crash as you approach 100% SNVB, because brown shrimp, white shrimp, and blue crabs use SNVB; estimates will decline to levels representative of densities in protected open water habitat. In reality, however, once a marsh complex essentially becomes an open bay, densities on SNVB may change; for example, Rozas and Zimmerman (2000) reported densities of white shrimp at Elmgrove Point of 5.6 shrimp/m² in marsh ponds and 0.0 shrimp/m² in the open bay. Declines in population estimates at high levels of SNVB were more apparent for blue crabs than for shrimps, because the density ratio between marsh edge and SNVB for blue crabs was relatively high (6.1) and the density decline away from the marsh edge was less steep than for shrimp. If these overall patterns reflect population changes associated with marsh degradation and fragmentation, our estimates suggest that shrimp and crab populations benefit during early stages of marsh disintegration, and that major population declines might not be expected until marshes are in late stages of disintegration.

Salt marshes are intertidal; and this characteristic has important implications for assessing relative value of marsh–water configurations for nekton (McIvor and

Rozas 1996, Connolly 1999). At low tide, most nekton are forced out of the marsh vegetation into adjacent subtidal areas (although see Kneib 1984, 1997b), and numerous ponds and creeks interspersed among islands of vegetation provide abundant low tide refuges. We sampled the Gang's Bayou marsh at high tide when the marsh surface was fully available, and the density estimates and distribution patterns we used for the vegetated marsh surface and SNVB are all based on this tidal stage. Obviously, the density patterns of nekton will change as the tide ebbs and the marsh surface is no longer flooded. However, marshes in the northwestern Gulf of Mexico are flooded for extended periods; monthly flooding durations for the marsh edge (or low elevation marsh surfaces) have been reported as high as 70–100% (Rozas and Reed 1993, Minello and Webb 1997, Whaley 1997, Rozas and Minello 1998, Castellanos and Rozas 2001). Marsh flooding is greatest in spring and fall, coinciding with periods of extensive marsh use by transient nekton species (Zimmerman and Minello 1984, Zimmerman et al. 2000). During six-week periods around our sampling of the Gang's Bayou marshes in the spring and fall, Whaley (1997) reported that the marsh surface at different distances from the edge was flooded 82–100% (1 m from edge), 64–99% (3 m), 58–99% (5 m), and 56–99% (10 m) of the time.

We examined the effects of adding edge to created marsh systems by simulating the addition of creeks in a 1-ha marsh island of solid vegetation. Results suggested that most benefits for shrimps and crabs could be realized by adding between 8–10 creeks/ha to a marsh (Fig. 8). Populations were highest when 16 creeks were added, but incremental population increases per creek at high creek densities were relatively low. The population levels reached in these simulations were higher than any estimates from the 39 sectors and about twice as large as the overall population estimates from the marsh complex at Elmgrove Point. This difference indicates that, despite having the appearance of extensive fragmentation, the natural marsh complex at Elmgrove Point did not approach the maximum amount of edge possible in a landscape.

Our data indicate that creek construction (or the addition of some edge) should be a high priority in the design of salt marshes to benefit brown shrimp, white shrimp, and blue crabs. The models show that there can be a negative effect on shrimp populations if a solid marsh is constructed without creeks and edge in an area that was once SNVB; a minimum of 1–2 creeks/ha (or a comparable amount of edge) is required to reach equivalent populations for SNVB. Additional creeks are needed (up to 5 creeks/ha) to reach shrimp and blue crab populations similar to those estimated for the Elmgrove Point marsh complex (Fig. 8). These conclusions assume that densities within created marsh vegetation are comparable to those in natural marshes, but densities of these species on the surface of created

marshes are only about half of those in natural marshes (Minello and Zimmerman 1992, Minello and Webb 1997, Rozas and Minello 2001). The construction of additional creeks might be considered as an option for improving the value of created marshes and making them more comparable to natural marsh systems in supporting these nekton species.

The construction of creeks in created marshes is an engineering challenge that poses functional, economic, and maintenance problems (Leopold et al. 1993, Williams and Zedler 1999, Zeff 1999, Simenstad et al. 2000). Relationships between tidal creeks and biological processes on the marsh surface are complex and geographically variable (Dame and Gardner 1993, Tyler and Zieman 1999, Zedler et al. 1999). An obvious problem with our simulated addition of edge in a created marsh is that natural marsh systems do not contain straight parallel tidal creeks. In addition to aesthetic considerations, meandering creeks may have functional attributes associated with their sinuosity (Zeff 1999). As apparent at Elmgrove Point, however, there are many configurations of marsh and water that can increase edge. The construction of marsh islands or terraces (Rozas and Minello 2001) should also be considered in attempts to maximize edge in wetland restoration projects.

We should expect the role of edge and fragment size in the overall ecology of a marsh system to be complex. The data presented here suggest that highly fragmented marshes with a large amount of edge support higher densities of transient species such as penaeid shrimps and blue crabs compared with solid unfragmented marshes. Minello et al. (1994) discussed possible reasons for high densities of these species in marsh edge habitat, and increased food, reduced predation (in relation to unvegetated bottom), and easy access to subtidal refuges may all be important. The impact of marsh fragmentation on resident species and on species diversity is less clear. There may be some parallels with avian fauna use of forest habitats, and research in these terrestrial systems indicates that fragmentation can affect predation intensity, overall abundance, and species diversity (Reese and Ratti 1988, Murcia 1995, Turner 1996, Donovan et al. 1997). Predation rates are relatively high near forest edges (Donovan et al. 1997); and similarly, relatively high abundances of predatory fishes, such as spotted seatrout *Cynoscion nebulosus* and red drum *Sciaenops ocellatus*, occur near marsh edges compared with open water or marsh interiors (Baltz et al. 1993, Minello 1999, Stunz 1999, Kneib 2000). Elevated predation intensity also occurs near edges of seagrass beds (Bologna and Heck 1999), but overall effects of edge and habitat fragmentation on nekton abundance and species diversity in seagrass habitats are unclear (McNeill and Fairweather 1993, Murphey and Fonseca 1995, Bologna and Heck 2000). Among other things, however, the intertidal nature of salt marshes is certain to complicate comparisons between marshes and either terrestrial or other marine ecosystems.

Literature Cited

Baltz, D. M., C. Rakocinski, and J. W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environmental Biology of Fishes **36**:109–126.

Baumann, R. H., J. W. Day, and C. A. Miller. 1984. Mississippi deltaic wetland survival: sedimentation versus coastal submergence. Science **224**:1093–1095.

Boesch, D. F., and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries **7**:460–468.

Bologna, P. A. X., and K. L. Heck. 1999. Differential predation and growth rates of bay scallops within a seagrass habitat. Journal of Experimental Marine Biology and Ecology **239**:299–314.

Bologna, P. A. X., and K. L. Heck. 2000. Impacts of seagrass habitat architecture on bivalve settlement. Estuaries **23**:449–457.

Britsch, L. D., and J. B. Dunbar. 1993. Land loss rates—Louisiana coastal plain. Journal of Coastal Research **9**:324–338.

Browder, J. A., H. A. Bartley, and K. S. Davis. 1985. A probabilistic model of the relationship between marshland-water interface and marsh disintegration. Ecological Modelling **29**:245–260.

Browder, J. A., L. N. May, A. Rosenthal, J. G. Gosselink, and R. H. Baumann. 1989. Modeling future trends in wetland loss and brown shrimp production in Louisiana using thematic mapper imagery. Remote Sensing of the Environment **28**:45–59.

Castellanos, D. L., and L. P. Rozas. 2001. Nekton use of submerged aquatic vegetation, marsh, and shallow unvegetated bottom in the Atchafalaya River Delta, a Louisiana tidal freshwater ecosystem. Estuaries **24**:184–197.

Clark, R. D., T. J. Minello, J. D. Christensen, P. A. Caldwell, M. E. Monaco, and G. A. Matthews. 1999. Modeling nekton habitat use in Galveston Bay, Texas: an approach to define Essential Fish Habitat (EFH). NOS Biogeography Program Technical Report Number 17. Silver Spring, Maryland and Galveston, Texas, USA.

Connolly, R. M. 1999. Saltmarsh as habitat for fish and nektonic crustaceans: challenges in sampling designs and methods. Australian Journal of Ecology **24**:422–430.

Dame, R. F., and L. R. Gardner. 1993. Nutrient processing and the development of tidal creek ecosystems. Marine Chemistry **43**:175–183.

Day, J. W., Jr., G. P. Shaffer, L. D. Britsch, D. J. Reed, S. R.

Hawes, and D. Cahoon. 2000. Pattern and process of land loss in the Mississippi delta: a spatial and temporal analysis of wetland habitat change. Estuaries **23**:425–438.

Deegan, L. A., J. E. Hughes, and R. A. Rountree. 2000. Salt marsh ecosystem support of marine transient species. Pages 333–365 *in* M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer Academic, Dordrecht, The Netherlands.

Delaney, T. P., J. W. Webb, Jr., and T. J. Minello. 2000. Comparison of physical characteristics between created and natural estuarine marshes in Galveston Bay, Texas. Wetlands Ecology and Management **8**:343–352.

Desmond, J. S., J. B. Zedler, and G. D. Williams. 2000. Fish use of tidal creek habitats in two southern California salt marshes. Ecological Engineering **14**:233–252.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology **78**:2064–2075.

Duffy, K. C., and D. M. Baltz. 1998. Comparison of fish assemblages associated with native and exotic submerged macrophytes in the Lake Pontchartrain estuary, USA. Journal of Experimental Marine Biology and Ecology **223**:199–221.

Faller, K. H. 1979. Shoreline as a controlling factor in commercial shrimp production. NASA Technical Memorandum **TM-72-732**:33.

Gabrysch, R., and L. S. Coplin. 1990. Land-surface subsidence resulting from ground-water withdrawals in the Houston-Galveston region, Texas, through 1987. U.S. Geological Survey Report of Investigations No. **90-01**.

Gagliano, S. M., K. J. Meyer-Arendt, and K. M. Wicker. 1981. Land loss in the Mississippi River deltaic plain. Transactions Gulf Coast Association of Geological Societies **31**:295–306.

Heck, K. L., Jr., and R. J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Pages 449–464 *in* V. S. Kennedy, editor. Estuarine perspectives. Academic Press, New York, New York, USA.

Kneib, R. T. 1984. Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* (Linnaeus) and *Fundulus luciae* (Baird). Journal of Experimental Marine Biology and Ecology **83**:41–51.

Kneib, R. T. 1994. Spatial pattern, spatial scale, and feeding in fishes. Pages 171–185 *in* D. J. Stouder, K. L. Fresh, and R. J. Feller, editors. Theory and application in fish feeding ecology. University of South Carolina Press, Columbia, South Carolina, USA.

Kneib, R. T. 1997*a*. The role of tidal marshes in the ecology of estuarine nekton. Oceanography and Marine Biology: an Annual Review **35**:163–220.

Kneib, R. T. 1997*b*. Early life stages of resident nekton in intertidal marshes. Estuaries **20**:214–230.

Kneib, R. T. 2000. Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. Pages 267–291 *in* M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer Academic, Dordrecht, The Netherlands.

Kneib, R. T., and S. L. Wagner. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. Marine Ecology Progress Series **106**:227–238.

Leopold, L. B., J. N. Collins, and L. M. Collins. 1993. Hydrology of some tidal channels in estuarine marshland near San Francisco. Catena **20**:469–493.

McIvor, C., and L. P. Rozas. 1996. Direct nekton use of intertidal saltmarsh habitat and linkage with adjacent habitats: a review from the southeastern United States. Pages 311–334 *in* K. F. Nordstrom and C. T. Roman, editors.

Estuarine shores: evolution, environments and human alterations. John Wiley & Sons, New York, New York, USA.

McNeill, S. E., and P. G. Fairweather. 1993. Single large or several small marine reserves—an experimental approach with seagrass fauna. Journal of Biogeography **20**:429–440.

Minello, T. J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. Pages 43–75 *in* L. R. Beneka, editor. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland, USA.

Minello, T. J., and J. W. Webb. 1997. Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. Marine Ecology Progress Series **151**:165–179.

Minello, T. J., J. W. Webb, R. J. Zimmerman, R. B. Wooten, J. L. Martinez, T. J. Baumer, and M. C. Pattillo. 1991. Habitat availability and utilization by benthos and nekton in Hall's Lake and West Galveston Bay. NOAA Technical Memorandum **NMFS-SEFC-275**.

Minello, T. J., and R. J. Zimmerman. 1992. Utilization of natural and transplanted Texas salt marshes by fish and decapod crustaceans. Marine Ecology Progress Series **90**:273–285.

Minello, T. J., R. J. Zimmerman, and R. Medina. 1994. The importance of edge for natant macrofauna in a created salt marsh. Wetlands **14**:184–198.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution **10**:58–62.

Murphey, P. L., and M. S. Fonseca. 1995. Role of high and low energy seagrass beds as nursery areas for *Penaeus duorarum* in North Carolina. Marine Ecology Progress Series **121**:91–98.

Perez Farfante, I., and B. Kensley. 1997. Penaeoid and sergestoid shrimps and prawns of the world; keys and diagnoses for the families and genera. Mémoires du Muséum National d'Histoire Naturelle, Tome 175. Paris, France.

Peterson, G. W., and R. E. Turner. 1994. The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. Estuaries **17**:235–262.

Reese, K. P., and J. T. Ratti. 1988. Edge effect: a concept under scrutiny. Transactions of the North American Wildlife and Natural Resources Conference **53**:127–136.

Rey, J. R., J. Shaffer, D. Tremain, R. A. Crossman, and T. Kain. 1990. Effects of re-establishing tidal connections in two impounded subtropical marshes on fishes and physical conditions. Wetlands **10**:27–45.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1991. Common and scientific names of fishes from the United States and Canada. Fifth edition. American Fisheries Society Special Publication **20**.

Rogers, D. R., B. D. Rogers, and W. H. Herke. 1994. Structural marsh management effects on coastal fishes and crustaceans. Environmental Management **18**:351–369.

Rozas, L. P. 1993. Nekton use of salt marshes of the Southeast region of the United States. Pages 528–537 *in* O. Magoon, W. S. Wilson, H. Converse, and L. T. Tobin, editors. Coastal Zone '93. Volume 2. Proceedings of the 8th Symposium on Coastal and Ocean Management. American Society Of Civil Engineers, New York, New York, USA.

Rozas, L. P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. Estuaries **18**:579–590.

Rozas, L. P., and T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries **20**:199–213.

Rozas, L. P., and T. J. Minello. 1998. Nekton use of salt marsh, seagrass, and nonvegetated habitats in a South Texas (USA) estuary. Bulletin of Marine Science 63:481–501.

Rozas, L. P., and T. J. Minello. 1999. Effects of structural marsh management on fishery species and other nekton before and during a spring drawdown. Wetlands Ecology and Management 7:121–139.

Rozas, L. P., and T. J. Minello. 2001. Marsh terracing as a wetland restoration tool for creating fishery habitat. Wetlands 21:327–341.

Rozas, L. P., and D. J. Reed. 1993. Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. Marine Ecology Progress Series 96:147–157.

Rozas, L. P., and R. J. Zimmerman. 2000. Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay estuary, Texas (USA). Marine Ecology Progress Series 193:217–239.

Sasser, C. E., M. D. Dozier, J. G. Gosselink, and J. M. Hill. 1986. Spatial and temporal changes in Louisiana's Barataria Basin marshes, 1945–80. Environmental Management 10:671–680.

Shafer, D. J., and W. J. Streever. 2000. A comparison of 28 natural and dredged material salt marshes in Texas with an emphasis on geomorphological variables. Wetlands Ecology and Management 8:353–366.

Simenstad, C. A., W. G. Hood, R. M. Thom, D. A. Levy, and D. L. Bottom. 2000. Landscape structure and scale constraints on restoring estuarine wetlands for Pacific Coast juvenile fishes. Pages 597–630 in M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer Academic, Dordrecht, The Netherlands.

Stunz, G. W. 1999. Causes and consequences of recruitment patterns in newly settled red drum (Sciaenops ocellatus). Dissertation. Texas A&M University, College Station, Texas, USA.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology 33:200–209.

Turner, R. E. 1997. Wetland loss in the northern Gulf of Mexico: multiple working hypotheses. Estuaries 20:1–13.

Tyler, A. C., and J. C. Zieman. 1999. Patterns of development in the creekbank region of a barrier island Spartina alterniflora marsh. Marine Ecology Progress Series 180:161–177.

Weaver, J. E., and L. F. Holloway. 1974. Community structure of fishes and macrocrustaceans in ponds of a Louisiana tidal marsh influenced by weirs. Contributions in Marine Science 18:57–69.

Whaley, S. D. 1997. The effects of marsh edge and surface elevation on the distribution of salt marsh infauna and prey availability for nekton predators. Thesis. Texas A&M University, College Station, Texas, USA.

Williams, A. B., L. G. Abele, D. L. Felder, H. H. J. Hobbs, R. B. Manning, P. A. McLaughlin, and I. Perez-Farfante. 1989. Common and scientific names of aquatic invertebrates from the United States and Canada: decapod crustaceans. American Fisheries Society Special Publication 17. Bethesda, Maryland, USA.

Williams, G. D., and J. B. Zedler. 1999. Fish assemblage composition in constructed and natural tidal marshes of San Diego Bay: relative influence of channel morphology and restoration history. Estuaries 22:702–716.

Zedler, J. B., J. C. Callaway, J. S. Desmond, G. VivianSmith, G. D. Williams, G. Sullivan, A. E. Brewster, and B. K. Bradshaw. 1999. Californian salt-marsh vegetation: an improved model of spatial pattern. Ecosystems 2:19–35.

Zeff, M. L. 1999. Salt marsh tidal channel morphometry: applications for wetland creation and restoration. Restoration Ecology 7:205–211.

Zimmerman, R. J., and T. J. Minello. 1984. Densities of Penaeus aztecus, P. setiferus and other natant macrofauna in a Texas salt marsh. Estuaries 7:421–433.

Zimmerman, R. J., T. J. Minello, and L. P. Rozas. 2000. Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the northern Gulf of Mexico. Pages 293–314 in M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer Academic, Dordrecht, The Netherlands.

Zimmerman, R. J., T. J. Minello, and G. Zamora. 1984. Selection of vegetated habitat by brown shrimp, Penaeus aztecus, in a Galveston Bay salt marsh. U.S. National Marine Fishery Service Fishery Bulletin 82:325–336.